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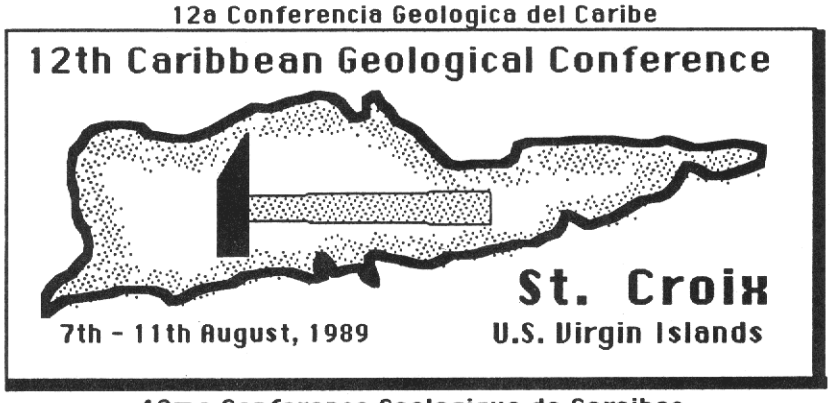

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TAPHONOMIC BIASING OF SUBFOSSIL ECHINOID POPULATIONS ADJACENT TO ST. CROIX, U.S.V.I.

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ABSTRACT

The distribution of live- and dead-echinoid populations occurring in forereef, reef and shallow subtidal environments in Smuggler's Cove and Rod Bay, St. Croix, was determined along 720 m and 50 m transects, respectively. Although echinoids are generally regarded as ubiquitous in shallow reef and adjacent environments, their distributions in Smuggler's Cove and Rod Bay are patchy. No intact tests of dead individuals were found associated with living populations and constituent particle analysis reveals a lack of correspondence between live echinoid distribution and sediment composition. Additional experiments conducted in the laboratory indicate that taxonomically-controlled differences in the size distribution of echinoid skeletal elements could play a role in determining their style of preservation. The lack of association of live and dead faunas as well as the results of field and laboratory experiments suggest that echinoids are quickly acted on by biostratinomic processes; their preservation, therefore, may require extraordinary circumstances. One such circumstance possibly occurred during 1983-84, when mass mortality decimated populations of *Diadema antillarum* adjacent to St. Croix. Tests and spines of *D. antillarum* were observed accumulating in seagrass beds immediately leeward of the reef tract in Smuggler's Cove in 1984. A piston core taken in 1988 from a seagrass bed leeward of the reef tract was analyzed centimeter by centimeter to determine if a horizon unusually rich in *Diadema* skeletal elements has been preserved as a result of the baffling and binding properties of the bed. No horizon is evident in the macro- or microscopic components of the core. The lack of a "*Diadema* spike" in an environment of net sediment accumulation suggests that individual tests of *Diadema* degrade so rapidly that increasing the amount of subfossil material as a consequence of the mass mortality alone was insufficient to preserve the event. Results of field and laboratory work are currently being synthesized into a predictive model for taphonomic overprint affecting fossil echinoids. A test of the model using literature-derived data of echinoid fossil occurrences is ongoing.

INTRODUCTION

The Class Echinoidea originated in the Ordovician and has a long and abundant fossil record. Their evolutionary history as interpreted through the fossil record is necessarily influenced by taphonomic bias. Kier (1977) demonstrated that, although both regular (generally epifaunal, radially symetrical) and irregular (generally infaunal, bilaterally symetrical) echinoids have rich fossil records, fossil regular echinoids are less abundant than their irregular counterparts. Kier also suggested that life habit and test construction of regular echinoids are, in part, responsible for their lower preservation potential. Thus, biostratinomic processes would be expected to particularly affect regular echinoids, rapidly obscuring any recognizable remains.

Schäfer (1972) described that, in the absence of rapid burial, echinoids disarticulate readily once decay sets in. Work by Greenstein and Meyer (1985a, b) extended this conclusion by demonstrating that scavengers greatly accelerate the disarticulation of the echinoid skeleton. Greenstein (1989) concluded that no recognizable signature of the mass mortality of *Diadema antillarum* remained in sediments surrounding a fringing reef in Bonaire, suggesting that increasing the amount of subfossil material alone was insufficient to overcome the taphonomic processes at work biasing the sedimentary record of the event. These studies intimate that each occurrence of a fossil regular echinoid is also a record of extraordinary taphonomic circumstances, a presumption contradicted by their abundance as fossils throughout most of the post-Paleozoic. Further study of taphonomic processes affecting populations of echinoids occurring in various reef subenvironments is clearly needed.

The reef and near-reef environments adjacent to St. Croix, U.S.V.I. are ideal areas in which to study echinoid taphonomy because of their abundant and

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diverse populations of regular echinoids. The echinoids *Diadema antillarum* (Family Diadematidae), *Eucidaris tribuloides* (Family Cidaridae) and *Echinometra lucunter* (Family Echinometridae) are particularly abundant. Although information on echinoid distribution and habits is presented in the classic studies of Clark (1919) and Kier & Grant (1965), no data comparing live echinoid distribution with that of subfossil echinoid material exist[1]. Here I determine the amount and nature of taphonomic bias affecting populations of these regular echinoids by comparing the distribution of living and dead individuals and conducting field experiments to determine the rate of decay and disarticulation of freshly-killed specimens. Finally, preliminary work is presented on the relative durability of the echinoids under study as determined by tumbling experiments.

METHODS

Population Censuses

Echinoid populations were censused along two transects constructed in Smuggler's Cove and Rod Bay (Fig. 1). The Smuggler's Cove site was selected because several reef and near-reef environments are present within a relatively short distance. A 720 m transect line was constructed heading due north from the Smuggler's Cove dock. Echinoids were counted in rocky shoreline, *Callianasa*-dominated sandy areas, *Thalassia*-dominated grass beds, patch reef, reef tract and shallow (water depth 1.5 m) and deep (water depth 12 m) forereef environments. At stations 60 m apart a 1 m^2 quadrat was placed adjacent to the transect line and live and dead echinoids within the quadrat were counted. The quadrat was then flipped over and another m^2 was censused. This process was repeated ten times at each station resulting in a census of a 1 x 10 m^2 "column" situated perpendicular to the transect line and occurring every 60 m. Surficial sediment samples were collected from the first quadrat censused at each station for later analyses to determine the contribution of echinoderm skeletal elements.

The Rod Bay site was selected because regular echinoids were observed to be particularly abundant. A 50 m transect was constructed, and the census proceeded in the same fashion as in Smuggler's Cove except that sampling stations were 10 m apart. Within the 50 m transect, rocky

[1]Although Serafy (1979) recorded the occurrence of live and dead echinoids collected by dredging along transects constructed adjacent to the Gulf Coast of Florida.

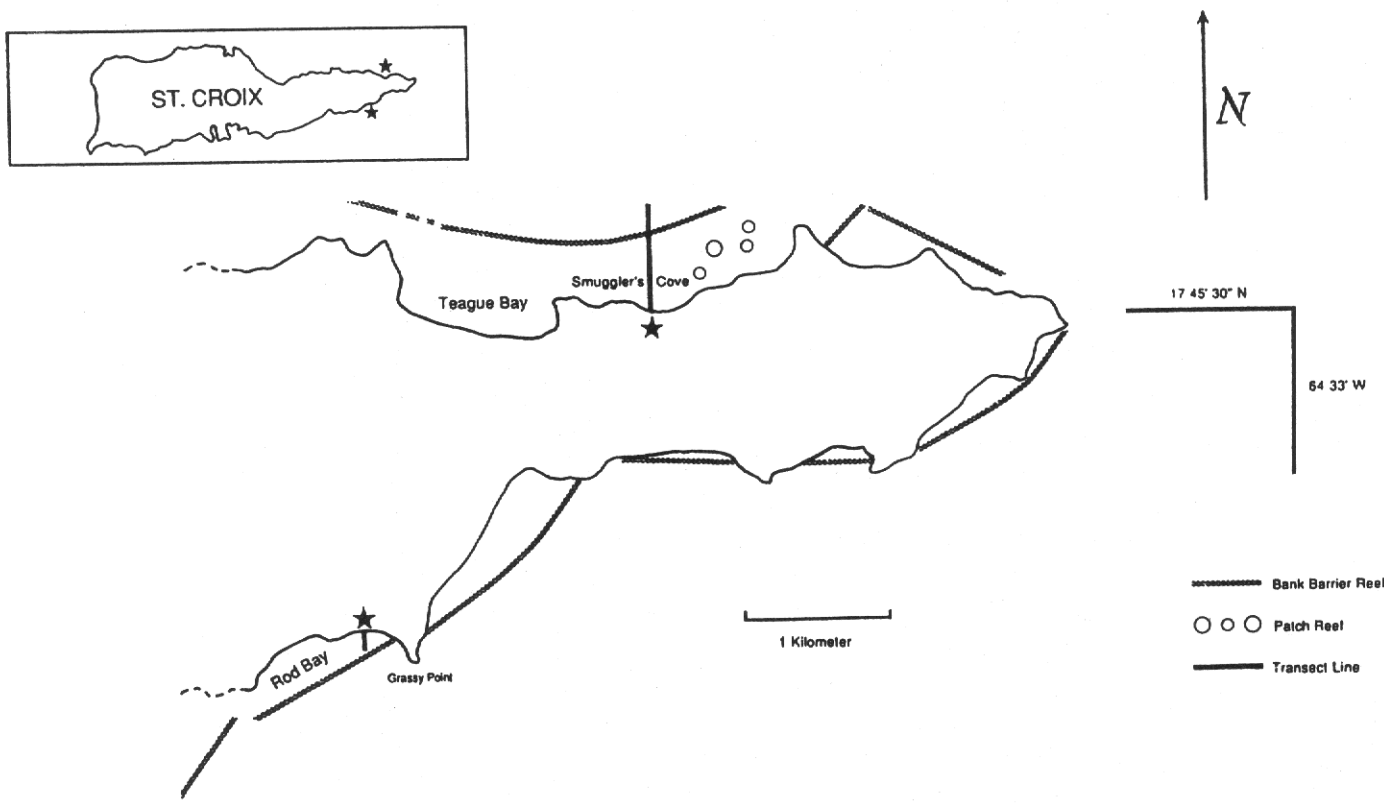
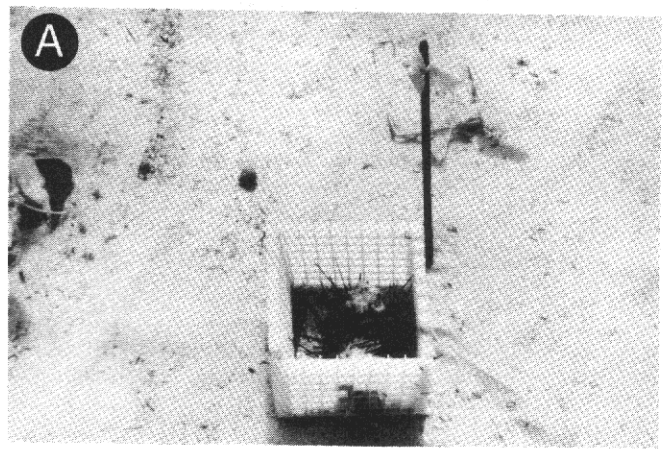


Figure 1- Transect localities adjacent to St. Croix. Each transect is marked with a star.

shoreline, *Thalassia*-dominated grass beds, a zone of coral-algal rubble and an environment of very small patch reefs were censused. Surficial sediment samples were also obtained.

Constituent Particle Analysis

Sediments obtained from stations along both transects were dried, impregnated with epoxy and ground into standard thin sections. Thus, all size fractions were represented in thin section to mitigate for the possibility that different echinoids would break down into different size fractions. The thin sections were point counted on a 1 mm^2 grid following the method of Ginsburg (1956). Echinoderm skeletal elements were counted by taking advantage of the unit extinction they exhibit in cross-polarized light, and their percent contribution to the sediment was calculated.



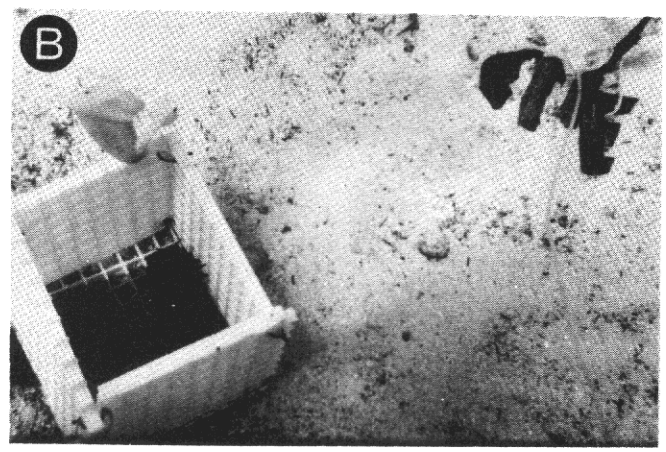


Figure 2- Echinoids placed in cages in the backreef (water depth 3 m) in Smuggler's Cove, A) Specimen of *D. antillarum*; B) Specimens of *E. lucunter* and *E. tribuloides*.

Field Experiments

Freezer-killed specimens of *Diadema antillarum* , *Eucidaris tribuloides* and *Echinometra lucunter* were placed in cages with open tops and a mesh size of 2 cm^2 . These "open" cages were used to contain the dead echinoids somewhat while leaving them exposed to large and small scavengers. The cages were placed on a wave-rippled, sandy substrate immediately behind the reef tract in Smuggler's cove in 4 m of water (Fig. 2). Additional cages were buried at 10 and 20 cm intervals in the sediment at the same location.

Tumbling Experiments

Specimens of *Echinometra lucunter* and *Diadema antillarum* were preserved in 95% ethanol in order to transport them intact from the field to the laboratory. The specimens were then placed in a 4:1 solution of bleach and water to oxidize all of the organic tissue contained within the skeleton . The resulting mass of spines, test and lantern elements was dried, weighed and placed in seawater in a baffled plastic tumbler attached to a variable speed motor (Fig. 3). Two trials of 1, 10 and 100 hours were run at 25 rpm for each echinoid. At the end of each trial the contents of the tumbler were wet-sieved through a stack of nested sieves and the >2mm, 1-2mm, 500μ-1mm and 125μ-500μ size fractions were isolated for analysis. Individual pieces of spine, test and lantern occurring in the three largest size fractions were counted and weighed. The 125μ-500μ size fraction was weighed only.

RESULTS AND DISCUSSION

Population Censuses

A total of 130 square meters were censused in Smuggler's cove (Fig. 4). Live *Echinometra*

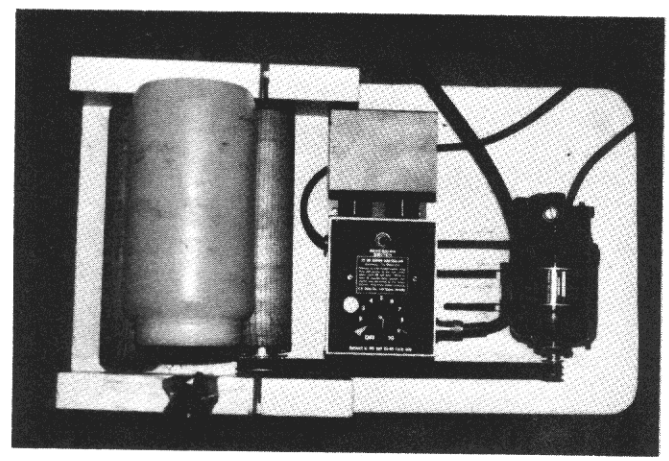


Figure 3- Tumbling device used in this study. Variable speed motor was set at 25 rpm.

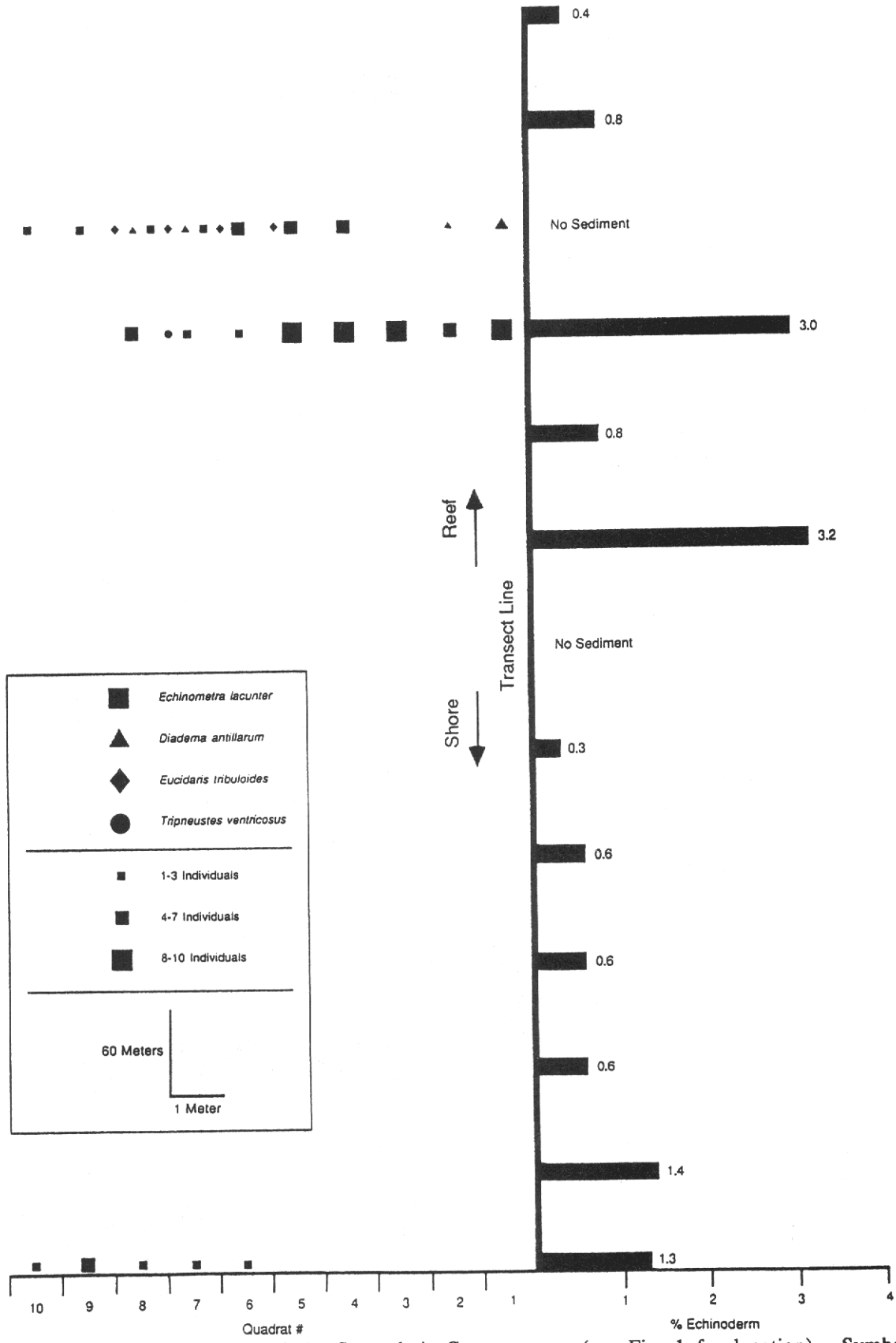


Figure 4- Schematic representation of the Smuggler's Cove transect (see Fig. 1 for location). Symbols to the left of the transect line indicate live echinoid abundance. Water depth reaches a maximum of 4 m in the backreef/ seagrass bed environment and 12 m in the fore-reef. Histogram to the right of the transect line shows the percent echinoderm grains point-counted in sediment samples.

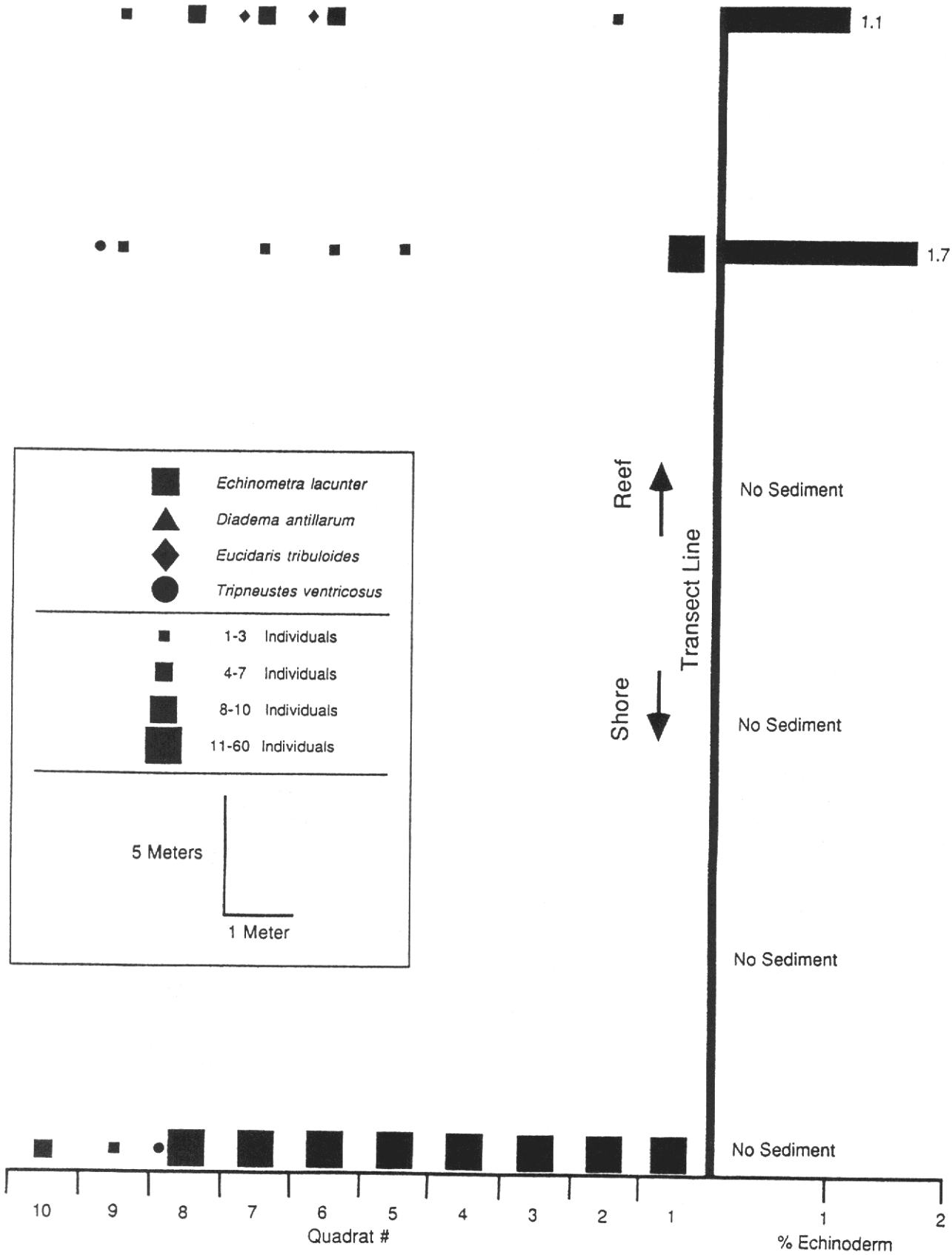


Figure 5- Schematic representation of the Rod Bay transect (see Fig. 1 for location). Symbols to the left of the transect line indicate live echinoid abundance. Maximum water depth along the transect is 1 m. Histogram to the right of the transect line shows the percent echinoderm grains point-counted in sediment samples.

lucunter were observed in low numbers along the rocky shoreline and no living echinoids were observed again until the same species was encountered in slightly higher numbers at the reef tract . Highest echinoid diversity occurred in the shallow forereef environment, with individuals of *D. antillarum*, *E. lucunter*, and *E. tribuloides* present in relatively low numbers. Live echinoids were not observed in the deeper forereef environment. No intact or partial tests of dead echinoids were observed in any quadrat studied along the entire transect.

Comparison of living and dead echinoids yielded essentially the same results in Rod Bay, where a census of a total of 60 square meters was conducted (Fig. 5). Although numbers of *Echinometra* were relatively high along the rocky shoreline (reaching a maximum of 59 individuals per square meter) no intact or partial tests of any echinoids were observed associated with the living fauna. Two individuals of *Tripneustes ventricosus* and four individuals of *Eucidaris tribuloides* were counted along with additional individuals of *Echinometra* at 40 and 50 meters along the transect, respectively. Dead echinoid material was not observed in any quadrat studied. In addition, very little sediment had accumulated in the area in which the transect was constructed, preventing collection at all but two stations.

Constituent Particle Analysis

Echinoderms at both localities are minor contributors to the sediment comprising, on average, 1.2% of the constituents and ranging from 0.3%-3.2%. The percentages of echinoderm skeletal elements in the sediment does not correspond to the distribution of echinoids (Figs. 4 & 5). In fact, the largest amount of echinoderm material occurred at a station where no echinoids were counted (Fig. 4). It should also be noted that the highest echinoid diversity and abundance occurred in an environment where no sediment was available to sample. Thus sediment compositon was an unreliable indicator of echinoid distribution in the two areas studied.

Field Experiments

The lack of correspondence of living echinoids to macro- and microscopic skeletal material suggests that the echinoids under study are rapidly acted on by biostratinomic processes. The field experiments were conducted to assess the rapidity with which this could occur. Within six days, all the echinoids placed in the back-reef environment in Smuggler's Cove were devoid of any organic material (Fig. 6). Few spines were observed within the cages and the tests of *E. tribuloides* and *E. lucunter* were filled with sediment and intact. The test of *D. antillarum* was also filled with sediment and appeared intact. Closer examination revealed, however, that the test had begun to separate along its ambulacral sutures. No elements of the Aristotle's Lantern of any of the echinoids were observed. Within 12 days, no spines were left within the cages and the tests of *Eucidaris* and *Echinometra* were still intact. The test of *Diadema* had completely disarticulated along its ambulacral sutures resulting in the presence of several large sections of interamb (Fig. 7).

The results of the field experiments help to partially resolve the lack of correspondence of the live and dead fauna. The rapid dissemination of spines and lantern elements from the cages indicates that they do not remain near the test that produced them. The patchy distribution of live echinoids observed in Smuggler's Cove and Rod Bay would therefore be expected to produce a scattered distribution of these skeletal elements which, even if time-averaged, would comprise a small proportion of the sediment.

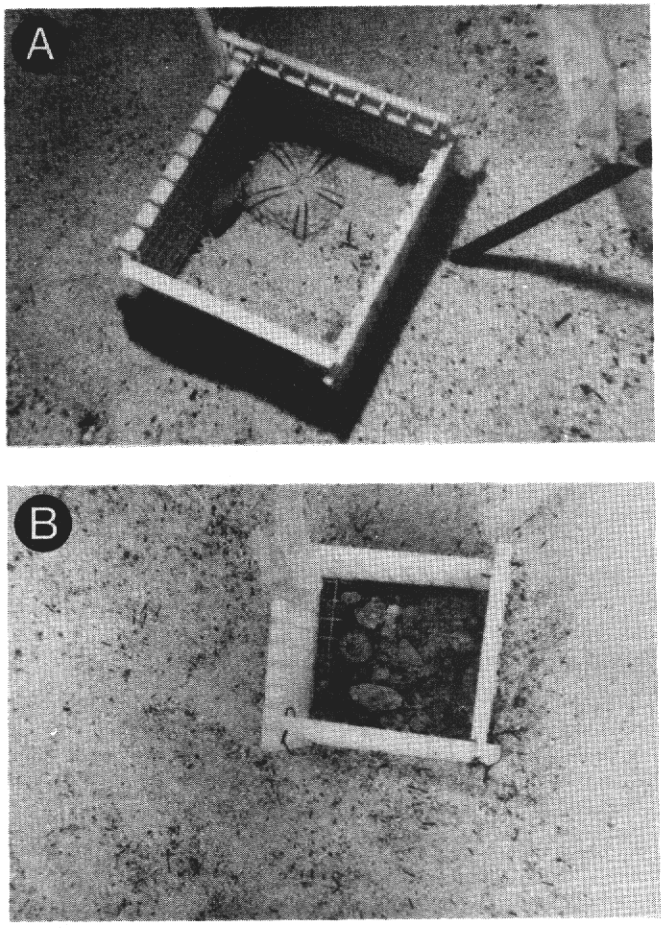


Figure 6- Echinoids in cages in backreef of Smuggler's Cove after six days, A) *D. antillarum*; B) *E. lucunter* and *E. tribuloides*. Note absence of organic tissues and spines.

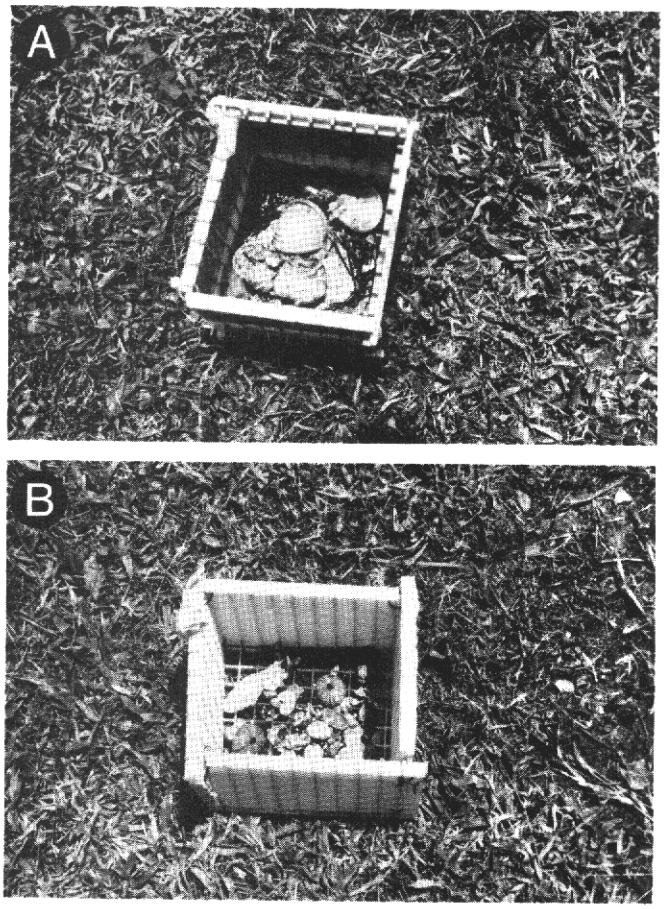


Figure 7- Cages containing echinoid specimens upon removal from the backreef in Smuggler's Cove. Cages were removed 12 days after the experiment was started, A) *D. antillarum*; B) *E. lucunter* and *E. tribuloides*. Note the difference in the condition of the tests.

The rapid degradation of the *Diadema* test relative to the other echinoids was expected. Of the echinoids studied, *Diadema* possesses the least durable test because very little interlocking of the stereom occurs at plate sutures (Smith, 1984). Thus no intact or partially intact tests of *Diadema* would be expected to occur in concert with live individuals, particularly since individuals of *Diadema* were observed in the shallow forereef environment where wave energy was quite high.

Echinometra represents the other end of the "durability spectrum" for the echinoids studied. A great deal of stereomic interlocking occurs across plate boundaries resulting in a test that is highly resistant to fracturing (Smith, 1984). However, no intact dead tests of this echinoid were found. Thus possession of a highly resistant test as well as relatively high abundance does not make the preservation of this echinoid any more likely than preservation of *Diadema* in the environments studied.

Tumbling Experiments

The purpose of the tumbling experiments was to assess whether any taxonomically-controlled difference in the breakdown of the echinoid skeleton contributes to taphonomic bias. Specimens of *Diadema* and *Echinometra* were selected because they represent the most fragile and the most sturdy of the echinoids studied. Data are expressed as weight percent of the entire skeleton to mitigate for the difference in size of the specimens. Average values of the two trials are presented.

The difference in test strength became apparent immediately as *Diadema* tests broke apart into the >2mm and 1-2mm size fractions within a few minutes of starting a tumbling trial whereas *Echinometra* tests remained intact in the >2mm size fraction after 100 hours of tumbling (compare Fig. 8 and Fig. 9). With increased tumbling time however,

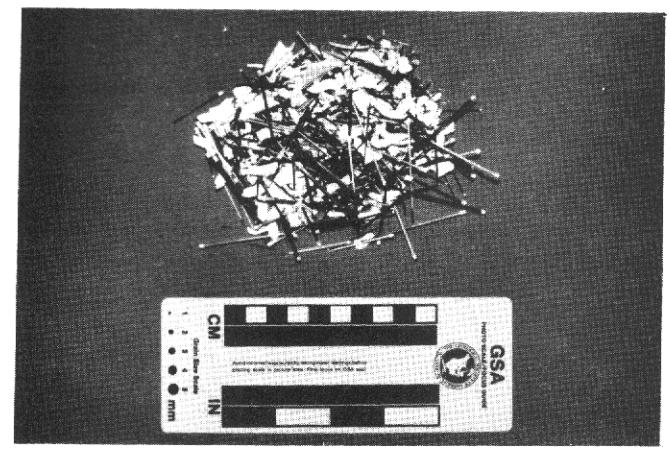


Figure 8- *D. antillarum* after one hour of tumbling. Note the considerable disarticulation of the test. The test was observed to disarticulate within minutes of starting the tumbler.

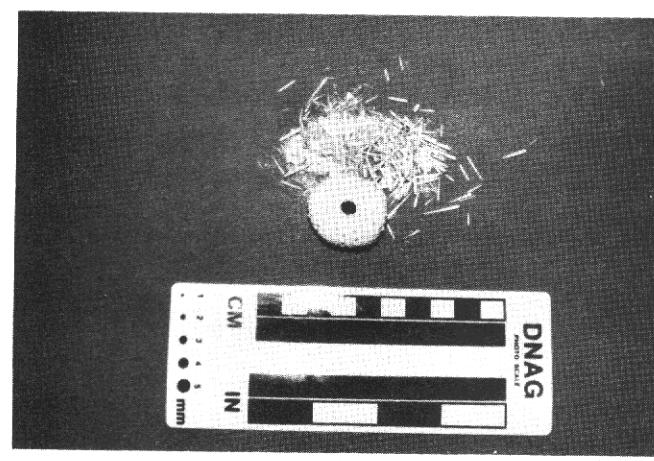


Figure 9- *E. lucunter* after one hour of tumbling. Note that the test is intact. Tests remained intact after tumbling periods of 100 hours.

there was little change in the proportions of either skeleton present in the three size fractions studied (Figs. 10 and 11). This indicates that no further abrasion of the skeletal elements occurred in the tumbler after initial disarticulation took place. Thus the fact that *Diadema* possesses a more fragile test than *Echinometra* only results in its much more rapid initial disarticulation and not in a greater proportion of the test contributing to the smaller size fractions. Spines of both echinoids are present in all the size fractions and lantern elements of both echinoids were present in only the >2mm size fraction (Figs. 12C and 13C).

The tumbling experiments suggest that, all things being equal, intact tests of *Echinometra*, larger lantern elements of both echinoids and spines of both echinoids should be apparent in close proximity to the live populations studied. Factors other than taxonomically-controlled patterns of test disarticulation are clearly at work to bias subfossil echinoid assemblages adjacent to St. Croix. Results of field work and laboratory experiments indicate that the echinoids studied are rapidly acted on by biostratinomic processes which initiate complex taphonomic histories. Although taxonomically-governed differences in skeletal strength do exist,

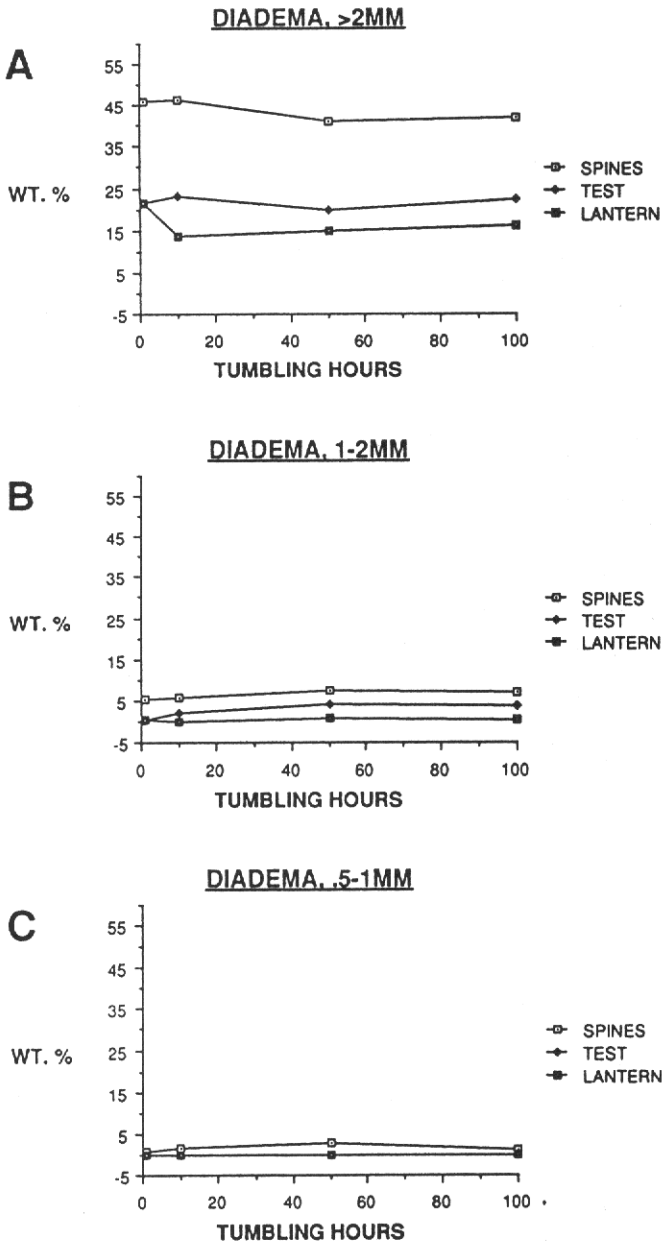


Figure 10-Tumbling results expressed as weight percent of the entire *Diadema* skeleton, A) >2 mm size fraction; B) 1-2 mm size fraction; C) 500 μ-1 mm size fraction.

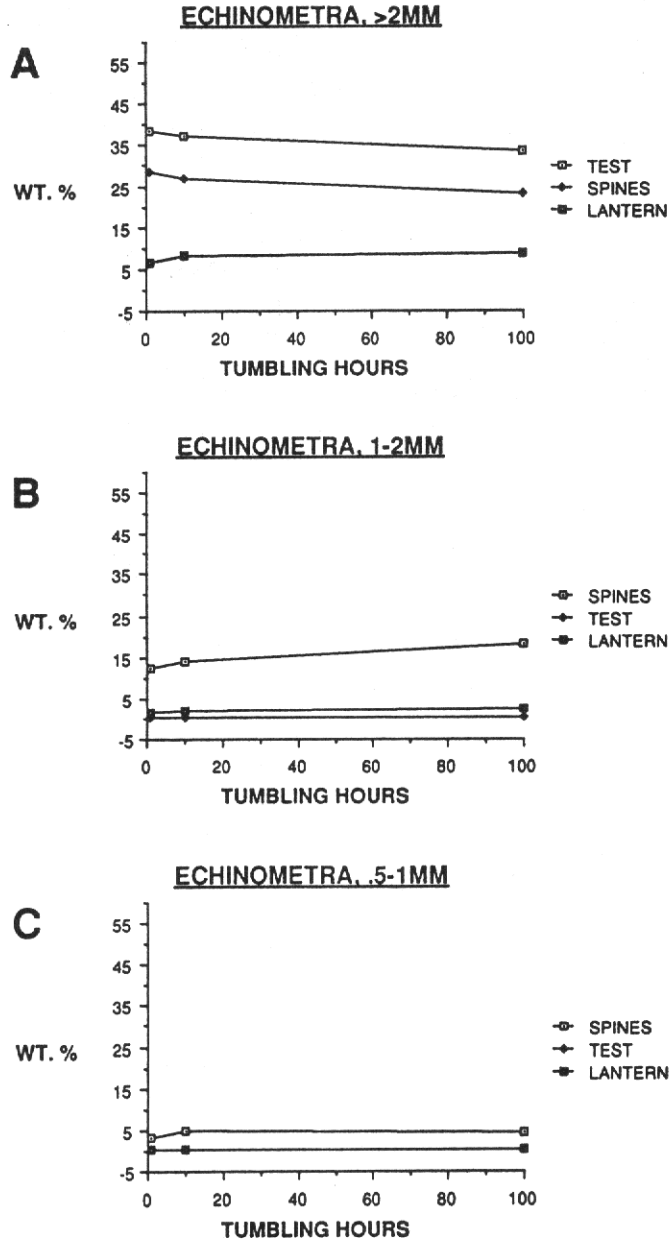


Figure 11-Tumbling results expressed as weight percent of the entire *Echinometra* skeleton, A) >2 mm size fraction; B) 1-2 mm size fraction; C) 500 μ-1 mm size fraction.

there is no *a priori* reason to assume that a stronger test makes preservation more likely in the environments studied in Smuggler's Cove. Thus it may be that, in the environments studied, extraordinary events are required to preserve the regular echinoids living there. Mass mortality of populations of *Diadema antillarum* occurred in St. Croix in 1984 and may have provided such an event.

Preservation of Echinoid Mass Mortality

During 1983-84 populations of *Diadema* were decimated, possibly by disease, throughout the Caribbean and tropical Western Atlantic (Lessios et al., 1984). Greenstein (1989) demonstrated that no signature of the event was present in surficial sediments accumulating in and around a fringing reef in Bonaire, Netherlands Antilles. However, active transport of sediment continually occurs in the area studied (Kobluk & Lysenko, 1984). In St. Croix, intact tests of *Diadema* were observed accumulating in sea grass beds leeward of the reef tract in Smuggler's Cove (Miller, pers. comm.). Sea grass beds are areas of net sediment accumulation (Ginsburg & Lowenstam, 1958). Thus one would expect that a sea grass bed might preserve, as a

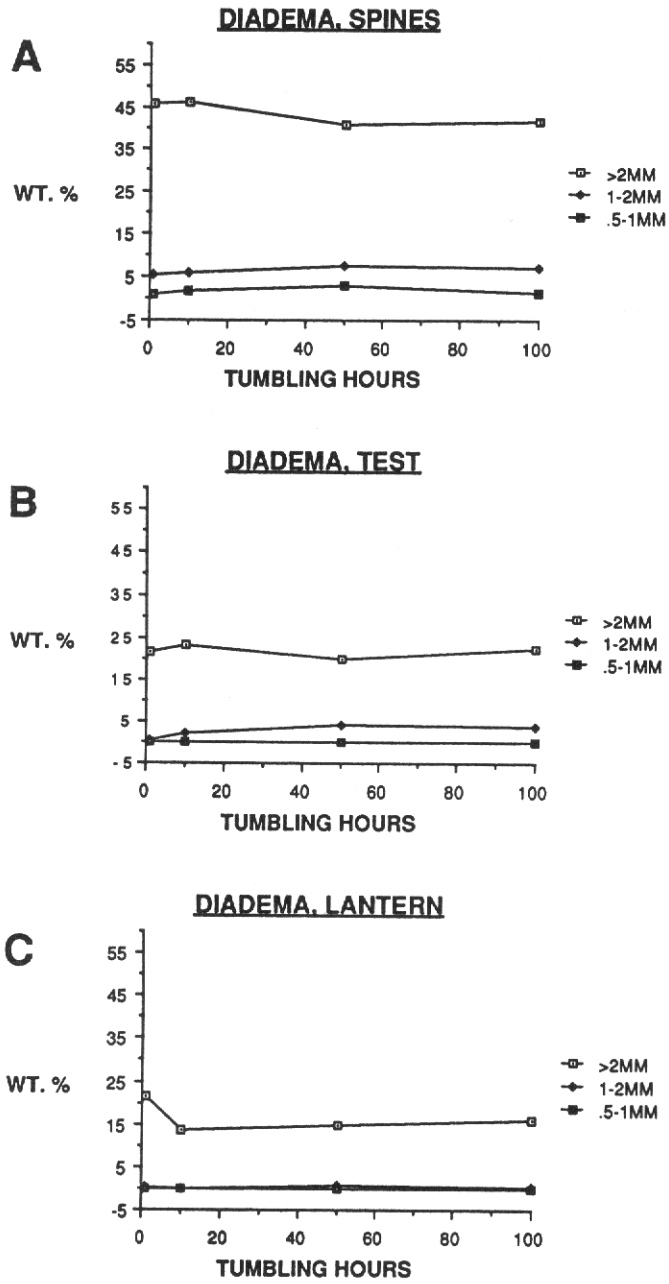


Figure 12-Tumbling results expressed as weight percent of the entire *Diadema* skeleton, A) spines; B) test plates; C) lantern elements.

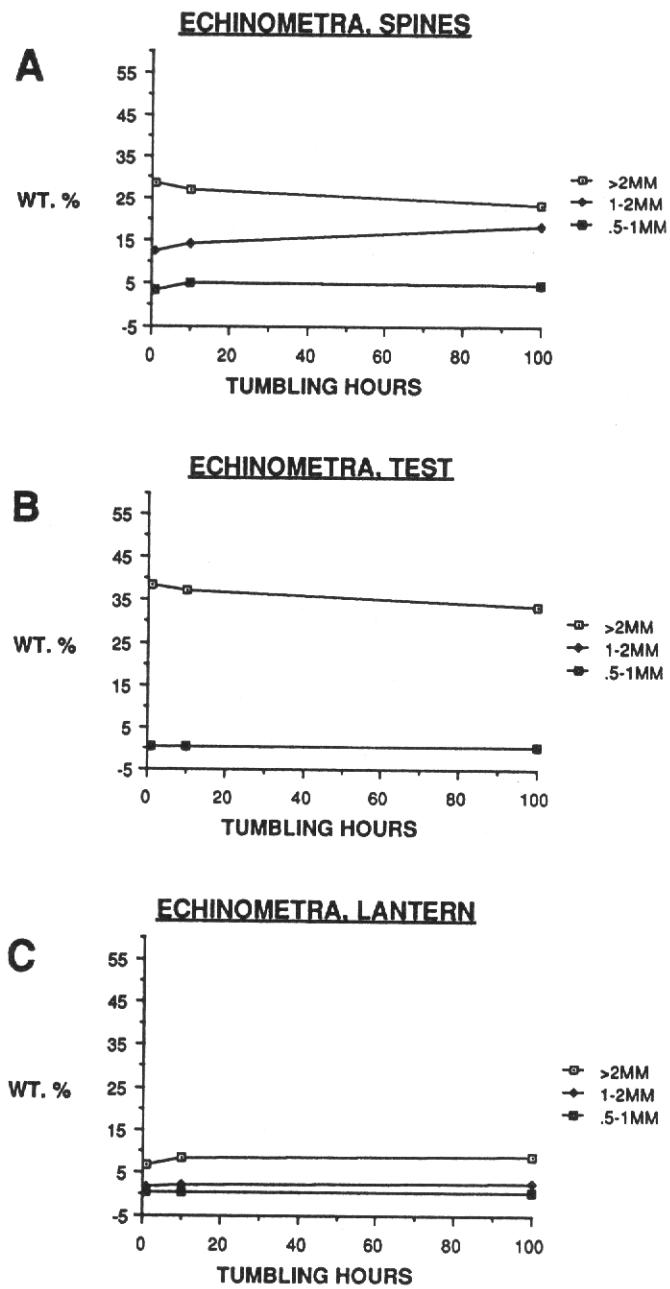


Figure 13-Tumbling results expressed as weight percent of the entire *Echinometra* skeleton, A) spines; B) test plates; C) lantern elements.

distinct horizon unusually rich in echinoderm material, an event that produced higher than normal amounts of subfossil echinoid material. In 1988 a 70 cm piston core was taken through a sea grass bed situated leeward of the reef tract in Smuggler's Cove to determine if such a horizon existed. The core was examined macroscopically on a centimeter scale for evidence of an echinoderm-rich layer in the larger size fractions and none was observed. Thin sections were made of material obtained at alternate-centimeter intervals and point counted using the same method described above.

Results of thin section analysis (Fig. 14) indicate that echinoderm grains comprise a small proportion of the sediment constituents in the core, ranging from 0.3-3.4%. The upper limit of a 95% confidence interval computed about the mean of the values is 1.95%. Approximately one-third of the values (10 of 33 samples) are higher than this value. Thus the variation in the amount of echinoderm material present does not produce an "echinoderm-spike". If the highest value of 3.4% is the result of the *Diadema* mass mortality, it is doubtful that the slight increase in echinoderm material would be recognizable in a stratigraphic succession. Thus, transport of innumerable intact tests of *Diadema* into an environment of net sediment deposition did not enhance their preservation potential.

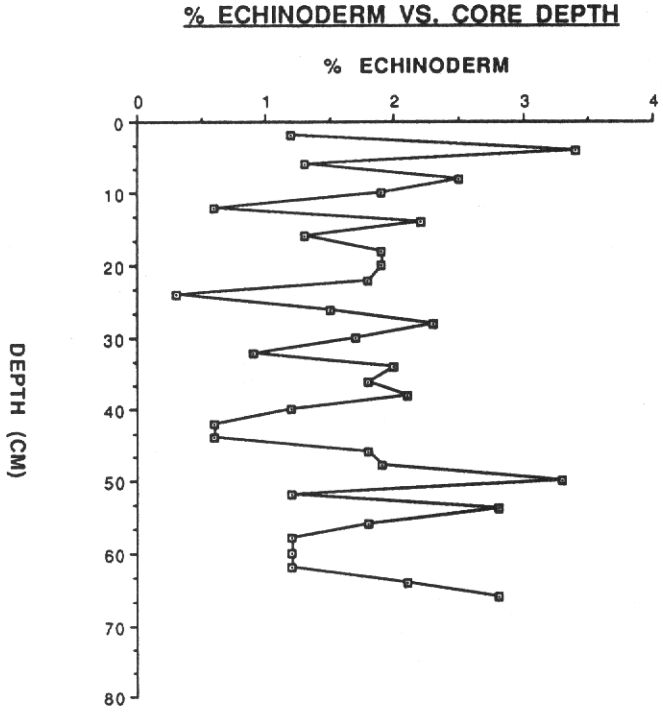


Figure 14-Percent echinoderm material vs. depth down core obtained from a seagrass bed leeward of the reef tract in Smuggler's Cove. Values obtained by point-counting.

IMPLICATIONS FOR ECHINOID FOSSIL RECORD

Results of the population censuses emphasize the rapidity with which populations of regular echinoids are reduced to essentially unrecognizable grains of carbonate sand. *Diadema* appears to be particularly vulnerable to taphonomic bias given the lack of signature of its mass mortality. The data obtained from the various facets of this study make it possible to predict the nature of the fossil records of each group represented by the species studied. Thus one would expect that in the absence of unusual taphonomic circumstances fossil species belonging to the Diadematidae might be represented by lantern or spine elements whereas intact tests of Echinometrids would more commonly be preserved. *Eucidaris tribuloides* and *Tripneustes ventricosus* were also subjected to rapid taphonomic bias in Smuggler's Cove. Although analysis of the disarticulation of their skeletons is ongoing, preliminary results indicate that fossil specimens of related forms would be expected to be preserved as skeletal fragments.

An analysis of the recorded occurrences of fossil species belonging to each family is currently underway. Type specimens of all species belonging to each of the four families are characterized according to preservational style, stratigraphic position and lithology of the enclosing unit. The literature-derived data, obtained for over 1000 species, will serve as a test of the predictions derived from the results of this study. Preliminary results suggest that, in addition to occurrences of well-preserved fossil species that are the result of extraordinary taphonomic circumstances (see for example Aslin, 1968, Bloos, 1973, Rosenkranz, 1971, Poborski, 1954 and Gill & Cobban, 1966), many species are described on the basis of fragmentary remains. This is particularly true of the Family Cidaridae, whose members comprise the longest and most diverse evolutionary history of the groups studied. Further analysis of the literature data will determine whether preservational style can be attributed to taxonomic, stratigraphic or lithologic factors.

CONCLUSIONS

1. The distribution of macro- and microscopic echinoid skeletal material does not reflect the distribution of living populations of *Diadema antillarum, Echinometra lucunter, Eucidaris tribuloides* and *Tripneustes ventricosus* in Smuggler's Cove or Rod Bay, St. Croix, suggesting that dead echinoids are rapidly acted on by biostratinomic processes.

2. Specimens of individual echinoids are divested of organic material, spines and lantern elements

within six days of death. In addition, tests of *Diadema antillarum* had begun to disarticulate along plate sutures.

3. High relative abundance and the possession of a relatively sturdy test do not make *Echinometra lucunter* any less vulnerable to taphonomic bias than the other echinoids studied.

4. Skeletons of *D. antillarum* disarticulate more rapidly than skeletons of *E. lucunter* when tumbled although no further breakdown of either skeleton occurs after initial disarticulation.

5. Results of tumbling experiments suggest that, in the absence of unusual taphonomic conditions, lantern elements and intact tests of Echinometrids may be expected to occur as fossils whereas spines, lantern elements and test fragments might represent Diadematids as fossils.

6. No echinoderm-rich horizon occurred in a seagrass bed core indicating that the generation of innumerable intact tests of *Diadema antillarum* and their transport into areas of net sediment accumulation was insufficient to preserve any record of widespread mass mortality.

7. Predictions concerning the preservational style of fossil species belonging to each family are currently being tested by an extensive review of the literature.

ACKNOWLEDGEMENTS

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REFERENCES

Aslin, C.J., 1968, Echinoid preservation in the Upper Estuarine Limestone of Bilsworth, Northamptonshire: Geological Magazine, v. 105, p. 506-518.

Bloos, G., 1973, Ein fund von seeigeln der Gattung *Diademopsis* aus dem Hettangium Württembergs und ihr Lebensraum: Stuttgarter Beitrage Naturklasse (B), v. 5, p. 1-25.

Clark, H.L., 1919, The distribution of the littoral echinoderms of the West Indies: Papers from the Department of Marine Biology of the Carnegie Institution of Washington, v. 12, p. 51-73.

Gill, J.R. & W.A. Cobban, 1966, The Red Bird section of the Upper Cretaceous Pierre Shale in Wyoming: U.S.G.S. Professional Paper 393-A, U.S. Government Printing Office.

Ginsburg, R.N., 1956, Environmental relationships of grain size and constituent particles in some south Florida sediments: American Association of Petroleum Geologists Bulletin, v. 40, p. 2384-2387.

Ginsburg, R.N. & H.A. Lowenstam, 1958, The influence of marine bottom communities on the depositional environment of sediments: Journal of Geology, v. 66, p. 310-318.

Greenstein, B.J., 1989, Mass mortality of the West-Indian echinoid *Diadema antillarum* (Echinodermata: Echinoidea): A natural experiment in taphonomy: Palaois, v. 4(5), p. 487-492.

Greenstein, B.J. & D.L. Meyer, 1985a, Mass mortality of the West Indian echinoid *Diadema antillarum*: A natural experiment in taphonomy: Geological Society of America Abstracts with Programs, v. 17(7), p. 598.

Greenstein, B.J. & D.L. Meyer, 1985b, Actuopaleontology of reef-dwelling echinoderms at Bonaire, Netherlands Antilles: Ohio Academy of Science Annual Meeting, Abstracts with Programs, v. 85(2), p. 19-20.

Kier, P.M., 1977, The poor fossil record of the regular echinoid: Paleobiology, v. 3, p. 168-174.

Kier, P.M. & R.E. Grant, 1965, Echinoid distribution and habits, Key Largo Coral Reef Preserve, Florida: Smithsonian Miscellaneous Collections, v. 149(6), p. 1-68.

Kobluk, D.R., and Lysenko, M.A., 1984, Carbonate rocks and coral reefs, Bonaire, Netherlands Antilles: Geological Association of Canada, Mineralogical Association of Canada Joint Annual Meeting Field Trip 13, 67 p.

Lessios, H.A., Robertson, D.R., and Cubit, J.D., 1984, Spread of *Diadema* mass mortality through the Caribbean: Science, v. 226, p. 335-337.

Poborski, S.J., 1954, Virginia formation (Triassic) of the St. George, Utah area: Geological Society of America Bulletin, v. 65, p. 971-1006.

Rosenkranz, D., 1971, Zur sedimentologie und Ökologie von echinodermen-lagerstätten: Neues Jahrbuch für Geologie und Palaöntologie Abhandlungen, v. 138, p. 221-258.

Schäfer, W., 1972, Ecology and paleoecology of marine environments: Oliver and Boyd, London, 568 p.

Serafy, D.K., 1979 Echinoids (Echinodermata: Echinoidea): Memoirs of the Hourglass Cruises, v. 5(Part 3), Florida Department of Natural Resources Marine Research Laboratory, 119 p.

Smith, A., 1984 Echinoid Palaeobiology: Special Topics in Palaeontology 1, George Allen and Unwin, London, 190 p.